

*RIFTIA PACHYPTILA*, NEW GENUS, NEW SPECIES,  
THE VESTIMENTIFERAN WORM FROM THE  
GALÁPAGOS RIFT GEOTHERMAL  
VENTS (POGONOPHORA)<sup>1</sup>

Meredith L. Jones

*Abstract.*—*Riftia pachyptila*, new genus, new species, is described from geothermal vents of the Galápagos Rift and from a geothermal area on the East Pacific Rise at 21°N. These vestimentiferan worms represent a new family, Riftiidae, in a new subphylum, Obturata, in the phylum Pogonophora. Differentiation from the two other vestimentiferan species is at the familial level and concerns the orientation of tentacular lamellae on the obturaculum, the number of openings of excretory ducts, and the relative lengths of certain body regions. A most curious structure, the trophosome, occupies much of the trunk region and is essentially a vascularized, bacteria-filled sac; it is also the site of deposition of crystals of elemental sulfur.

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In 1966 specimens of a worm, *Lamellibrachia barhami* Webb, were collected off the coast of California at a depth of 1,125 m. These animals, designated as a new class of Pogonophora by Webb (1969a), have subsequently been the object of continuing detailed research by him (Webb, 1969b, c, 1971, 1975, 1977). Inclusion in the Pogonophora was based “. . . primarily on the shape, structure, and protein content of the tube,” as well as “. . . distinctive pogonophoran characters: the very long trunk region, the metasoma, and the absence of a gut” (Webb, 1969a, p. 41). Webb’s new pogonophoran class, Afrenulata, was characterized merely by the lack of a bridle (frenulum), while his new order, Vestimentifera, was erected on the basis of: 1. Simple paired excretory ducts, without connections with the tentacular coelom, which open exteriorly by a single median excretory pore at the base of the “tentacular crown”; 2. An undifferentiated trunk, provided with papillae; 3. A tentacular crown formed of numerous fused tentacles surrounding a paired, centrally placed “lophophoral organ,” which is in turn surrounded by a number of tentacular sheaths; 4. A so-called vestimental region between the tentacular crown and the trunk, provided with lateral folds which meet to form a vestimental chamber between the vestimentum and the tube; and 5. Genital apertures which open into the

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vestmental chamber, with male apertures provided with ciliated grooves. A second collection of *L. barhami* was reported by Webb (1977) from off the coast of Oregon.

In 1970 a second species of vestimentiferan was collected from a depth of 500 m on the continental slope off Guyana. *Lamellibrachia luymesii* van der Land and Nørrevang was described from a single male specimen, and has been reported upon in two papers (van der Land and Nørrevang, 1975, 1977). Specific differences between *L. barhami* and *L. luymesii* cited by van der Land and Nørrevang (1975) were: 1. The relative length of the vestimental region; 2. The number of tentacular sheaths; 3. The relative proximity of male genital apertures; 4. The structure of the tube; and 5. The presence of various grooves and lines of pigment on certain parts of the trunk and vestimentum.

The descriptions of the two species of *Lamellibrachia* point up a continuing controversy concerning the dorso-ventral orientation of the Pogonophora. On the one hand Webb considers the nerve cord to be dorsal, while van der Land and Nørrevang assume that it is ventral; the former view implies a relationship to the hemichordates *et al.*, and the latter, to the annelids. Three sets of neutral terms have been suggested: "neural" and "tentacular," "neural" and "antineural," "adneural" and "antineural," (Southward, 1975a, b; Anon., 1975, p. 143, respectively). In this paper I decline to use the neutral terms of orientation, for there is no unequivocal distribution of tentacles in the vestimentiferans and, while "neural," "adneural," and "antineural" are unequivocal, I find them awkward and I suspect that they may be susceptible to confusion. As will be noted below, it is my opinion that the vestimentiferans, as well as the Pogonophora, stand in close relationship to the Annelida and I follow van der Land and Nørrevang in considering the nerve cord to be ventral and the major blood vessel, provided with a thick muscular layer, to be dorsal.

In 1977 and 1979 during expeditions to the Galápagos Rift and East Pacific Rise areas the submersible *Alvin* obtained a number of vestimentiferans which are the subject of this paper. At the Galápagos sites, water coming from geothermal vents may be as warm as 23°C and may contain hydrogen sulfide to the extent of 160  $\mu$ mole per liter, and, at temperatures above 10°C, the vent waters are anoxic; ambient temperature of bottom water near the vents is about 2°C, it is oxygenated, and there is no hydrogen sulfide present (Corliss *et al.*, 1979). A total of 63 worms, collected at three geothermal vents in the Galápagos Rift area and one vent on the East Pacific Rise, have been deposited in the collections of the Division of Worms, National Museum of Natural History (USNM), Smithsonian Institution, and these form the basis for the following description. Paraffin sections were cut at 5  $\mu$ m and stained with routine staining procedures indicated below. The identity of sulfur crystals was confirmed by an ARL-SEMQ electron microprobe



and by X-ray diffraction utilizing CuK X-radiation (nickel-filtered) with a Gandolfi 114.6 mm camera and a polycrystalline sample.

### Riftiidae, new family

*Type-genus*.—*Riftia*, new genus.

*Diagnosis*.—Vestimentiferans with tentacular lamellae at right angles to obturaculum; without tentacular sheaths; obturaculum at least 11% of total length; with separated, paired, external openings of excretory ducts; with essentially cylindrical tube.

### *Riftia*, new genus

*Type-species*.—*Riftia pachyptila*, new species.

*Gender*.—Feminine.

*Diagnosis*.—Characters of the family (above).

*Etymology*.—From Danish and Norwegian, *rift* (rent, fissure) + *-ia*, in reference to the Galápagos Rift.

### *Riftia pachyptila*, new species

Figs. 1–4

Worm(s).—Ballard, 1977:41, 43 (with fig.).—Anon., 1979:11 (with fig.).—The Editor, 1979:680, 681 (fig.).—Ballard and Grassle, 1979:689 (with fig.).—Schlee, 1979:41.

Tube worm(s).—Corliss and Ballard, 1977:441 (with fig.), 449.—Corliss *et al.*, 1979:1079.—Schlee, 1979:42 (with fig.).—The Editor, 1979:688.—Ballard and Grassle, 1979:699 (with fig.), 705 (fig.).—RISE Project Group, 1980:1421, 1432.

Pogonophora(ns).—Corliss and Ballard, 1977:441 (with fig.).—Corliss *et al.*, 1979:1075, 1079–1080, figs. 4, 5.

Vestimentifera(ns).—Corliss *et al.*, 1979:1079.—Ballard and Grassle, 1979:689 (with fig.).—Galápagos Biology Expedition Participants, 1979:6 (with fig.), 7, 8.—Jannasch and Wirsén, 1979:592, 594–595.—RISE Project Group, 1980:1424, fig. 5.—Hekinian *et al.*, 1980:1435.—Terwilliger *et al.*, 1980:531 *et seq.*

*Diagnosis*.—Characters of the family (above).

*Etymology*.—From Greek, *pachys* (thick) + Greek, *ptilon* (feather), in reference to the aspect of the anterior plume of the worm (combination treated as an adjective).

*Type-locality*.—“Rose Garden” geothermal vent (RG), Galápagos Rift (00°48'15"N; 86°13'29"W), 2,450 m depth.

*Other localities of paratypes*.—Galápagos Rift—“Dandelions” geothermal vent (D) (00°47'42"N; 86°08'00"W), 2,496 m depth; “Garden of Eden”

geothermal vent (GE) (00°47'42"N; 86°07'44"W), 2,485 m depth. In addition, worms have been noted, but not collected, at "Mussel Bed" geothermal vent (00°48'06"N; 86°07'00"W), 2,490 m depth. East Pacific Rise geothermal vent (EPR) (20°51'00"N; 109°04'54"W), 2,595 m depth.

*Material examined.*—Holotype (USNM 59951), RG, Alvin Dive (AD) 889, 14 Feb 1979, adult female. Paratypes: 1 adult, D, AD 723, 27 Feb 1977; 1 sectioned adult (USNM 59953), 1 sectioned juvenile (USNM 59954), 8 adults and juveniles (USNM 59955), GE, AD 733, 16 Mar 1977; 3 adults (USNM 59956), GE, AD 884, 25 Jan 1979; 1 adult (USNM 59957), 1 sectioned young adult (USNM 59958), 1 young adult (USNM 59959), 3 sectioned juveniles (USNM 59960–62), 7 juveniles (USNM 59963), RG, AD 889, 14 Feb 1979; 1 adult (USNM 59964), EPR, AD 915, 22 Apr 1979; 2 adults (USNM 59965), RG, AD 983, 30 Nov 1979; 2 adults (USNM 59966–67, RG, AD 984, 1 Dec 1979; 1 adult (USNM 59968), RG, AD 988, 5 Dec 1979; 1 adult, 1 young adult (USNM 59969), 1 adult, 1 young adult, 1 juvenile (USNM 59970), 1 adult, 2 young adults (USNM 59971), 1 adult, 1 juvenile (USNM 59972), 7 adults (USNM 59973–79), RG, AD 990, 7 Dec 1979; 1 adult, 2 young adults (USNM 59980), 2 adults (USNM 59981–82), GE, AD 993, 10 Dec 1979. Non-Types: 2 empty tubes (USNM 59996–97), GE, AD 983, 30 Nov 1979; 1 empty tube (USNM 59998), RG, AD 990, 7 Dec 1979; 1 empty tube with adult fragment and 7 juveniles (USNM 59999), GE, AD 993, 10 Dec 1979.

*Description.*—Dimensions, relative lengths and certain meristic characters of the holotype and a representative series of paratypes are listed in Table 1.

With four body regions: (1) Anterior tentacular plume on obturaculum; (2) Winged vestimentum; (3) Trunk; (4) Segmented posterior opisthosome (terminology: Webb, 1969a; van der Land and Nørrevang, 1975, 1977) (Fig. 1B).

Central axial obturaculum of plumed region paired and fused, splayed apically (Fig. 1C); with non-ciliated dorsal groove and ventral ridge along length (Fig. 2B); with tentacular lamellae perpendicular to axis, extending nearly to anterior tip, giving impression of thick feather (Fig. 1D); paired

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Fig. 1. *Riftia pachyptila* (A: USNM 59999; B: USNM 59951; C, E: USNM 59957; D: USNM 59956). A, Tube with four young individuals attached; apical aperture, upper left; closed basal end, right center; tube cut to obtain animal; folds in tube, during initial storage/preservation, give misleading appearance to relatively uniform tube diameter; B, Overall view of holotype; C, Obturacular plume, lateral view; splayed distal end, above; D, Same, ventral view; E, Vestimentum, ventral view; BN: bifurcated ventral nerve; JU: juvenile; LT: large tentacle; OB: obturaculum; OP: opisthosome; TR: trunk; VC: ventral ciliated field; VE: vestimentum; VR: ventral ridge; VW: vestimental wing; YA: young adult. Scale bars (lower right)—A, B: 10 cm; C–E: 5 cm.



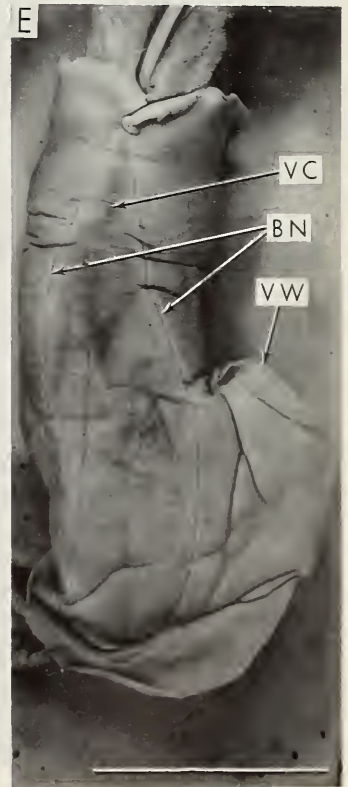
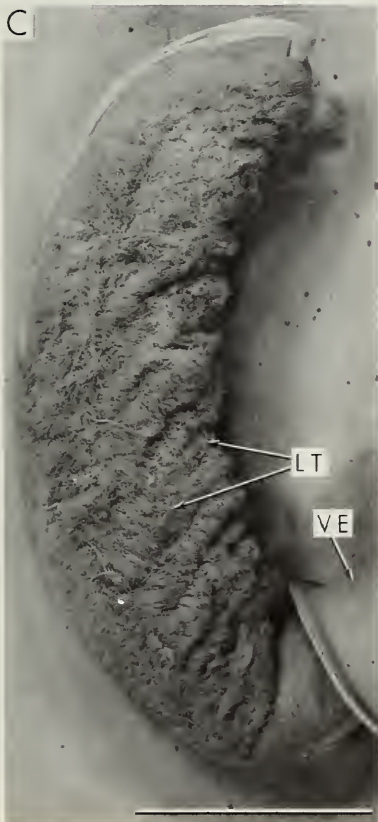
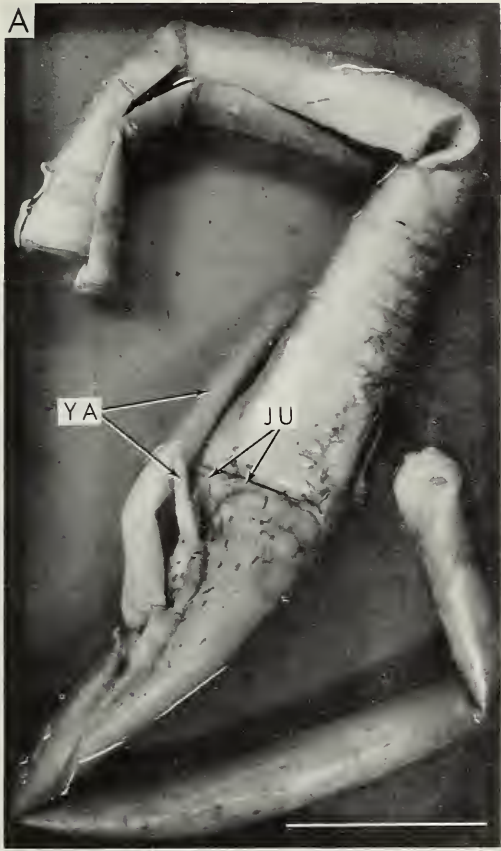


Table 1.—*Riftia pachyptila*: Comparison of specimens of various lengths showing relative lengths of obturaculum (OB), vestimentum (VE), trunk (TR), and opisthosome (OP), with numbers of paired tentacular lamellae and of opisthosomal segments.

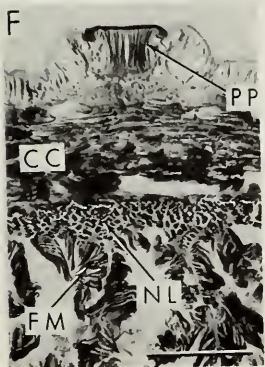
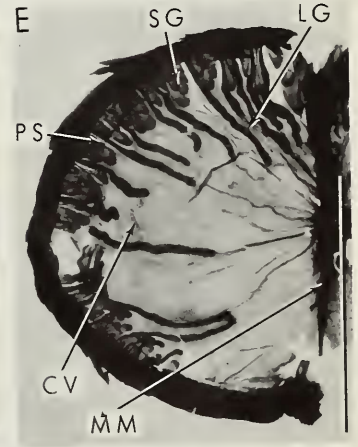
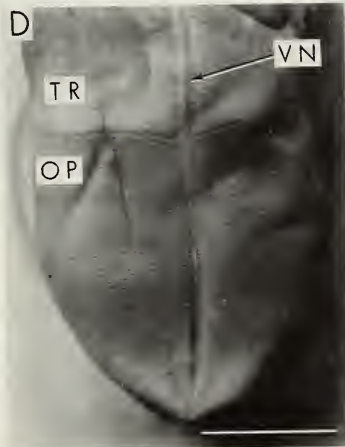
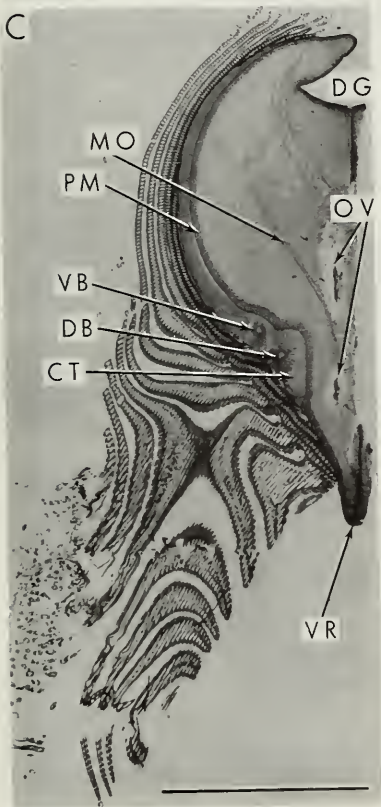
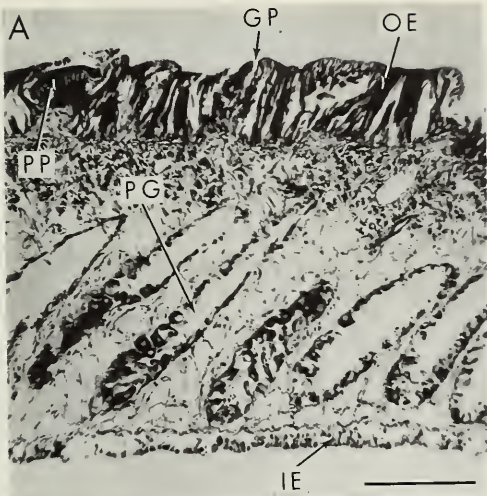
Cat. number	Sex	Percentage body length				Total length (mm)	No. tent. lamellae	No. op. segs.
		OB	VE	TR	OP			
USNM 59951	♀	11	7	80	2	1,502.00	334	96
USNM 59957	♂	16	13	69	3	1,056.00	302	103
USNM 59964	♀	34	13	49	3	513.00	257	86
USNM 59952	♀	17	17	59	7	320.00	170	85
USNM 59955	♀	22	18	53	7	273.00	193	74
USNM 59955	♀	26	22	45	7	215.00	166	66
USNM 59959	♀	26	12	56	6	199.00	116	72
USNM 59953	♂	22	16	55	6	171.00	113	95
USNM 59959	♀	27	11	57	5	169.00	111	78
USNM 59958	♀	24	14	56	6	111.00	113	73
USNM 59959	♂	29	13	49	9	77.00	95	82
USNM 59959	♂	27	13	53	7	55.00	63	71
USNM 59954	?	34	24	30	13	15.50	39	36
USNM 59963	?	30	26	33	21	6.10	12	19
USNM 59963	?	33	22	28	17	6.00	23	25
USNM 59963	?	28	19	35	19	4.30	8	18
USNM 59960	?	28	18	34	20	1.60	1?	11
USNM 59963	?	35	17	29	19	0.75	—	2+

halves of apical split end forming operculum upon withdrawal into tube. In life vestimentum with dorsolateral flaps/wings overlapping one another within tube, with free anterior margin of flaps meeting and slightly overlapping ventrally (Fig. 1E); free posterior margin of flaps continuous and entire, ventrally (Fig. 1B, E); paired genital apertures at posterior third of dorsal

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Fig. 2. *Riftia pachyptila* (A: USNM 59958; B, C, E–G: USNM 59953; D: USNM 59951). A, Vestimental wing, transverse section; Masson's Trichrome stain; outer surface when overlapped, above; inner surface, below; B, Tentacular lamella, complete, from mid-region of obturaculum; obturaculum, upper right; Mallory's Triple stain (ML); C, Obturaculum with associated tentacular lamellae, transverse section; Chlorazol Black; D, Opisthosome, ventral view; E, Opisthosomal septum, complete, from one side (ML); F, Trunk body wall, transverse section, showing plaqued papilla; Toluidine Blue; G, Trunk, transverse section (ML). CC: circular muscle/connective tissue; CO: coelom; CT: compartmented tissue; CV: connecting vessel; DB: anterior branch of dorsal vessel; DG: dorsal groove; DM: dorsal mesentery; DV: dorsal vessel; FM: "feather" longitudinal muscle; GP: gland papilla; IE: inner epithelium; LG: "long" gland; LT: large tentacle; MM: medial mesentery; MO: muscle strands of obturacular matrix; NL: "normal" longitudinal muscle; OE: outer epithelium; OP: opisthosome; OV: obturacular vessel; PG: pyriform gland; PM: parasagittal muscle; PP: plaqued papilla; PS: partial septum; SG: "short" gland; TP: trophosome; TR: trunk; TS: testes; VB: anterior branch of ventral vessel; VM: ventral mesentery; VN: ventral nerve; VR: ventral ridge; VV: ventral vessel. Scale bars (lower right) A, F: 100  $\mu$ m; B, C, E, G: 5 mm; D: 10 mm.





surface in both sexes; male aperture associated with ciliated ridges, converging but not meeting anteriorly; female apertures lacking ciliated ridges; ventral ciliated field somewhat pear-shaped, delimited by paired ventral nerves and neurular tubes (Fig. 1E); papillar openings of internal pyriform glands on surface, apart from ventral ciliated field, and on outer surface of overlapped flaps (Fig. 2A); dorsal cavity formed by overlapping flaps nearly lacking such papillar openings, with cuticle, lacking specialized epithelium. Trunk with similar papillae, with united single ventral nerve and neurular tube extending throughout length (Figs. 2G, 3A). Opisthosome with variable number of segments, ending in rounded posterior tip (Fig. 2D); anterior segments (about  $\frac{1}{3}$  length), each completely encircled with paired single rows of setae, becoming incomplete posteriorly.

No setae on vestimentum or trunk; setae with long shafts with two toothed areas extending free of body surface; many teeth in posterior area, pointing anteriorly; fewer in anterior area, pointing posteriorly; identical with girdle setae of Pogonophora (Fig. 4B); no peg-like setae.

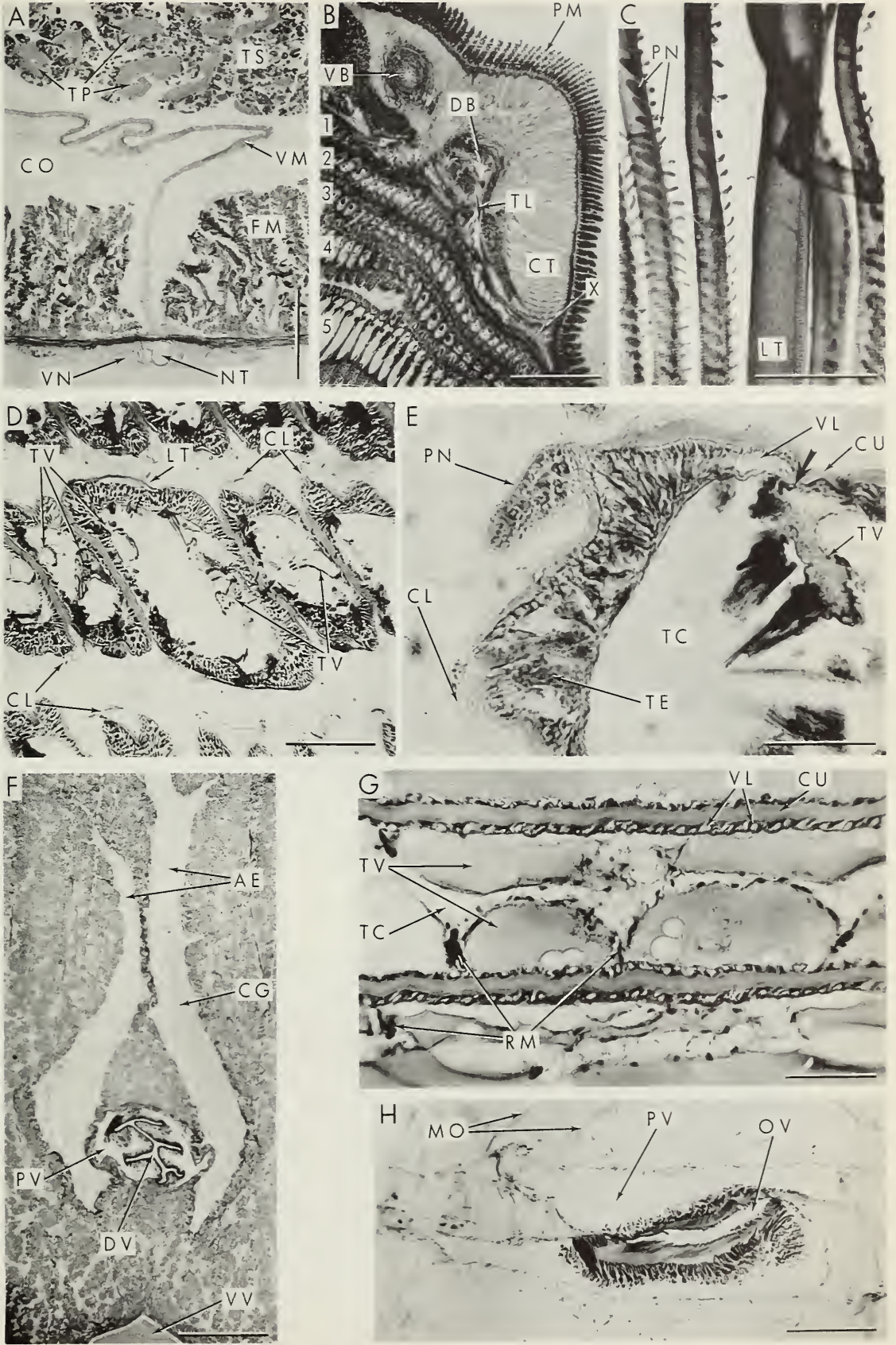
Papillae most numerous on outer surface of vestimental wings and on posterior trunk, progressively fewer papillae anteriorly along trunk, very few papillae on dorsal surface of vestimentum and inner surface of wings; papillae with plaques about three to five times more numerous than those without plaques, latter probably exit for secreted tube material.

Tube white, flexible, extremely sturdy, essentially cylindrical (Fig. 1A); basally blind-ending, approximate shape of opisthosome; apical opening thinning to apertural margin; main part of tube commonly 2–3 mm thick; tube material laid down incrementally forming rudimentary "collars" or

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Fig. 3. *Riftia pachyptila* (A–E, G–H: USNM 59953; F: USNM 59958). A, Trunk, ventral body wall, transverse section; Toluidine Blue; B, Compartmented tissue adjacent to obturacular matrix and basal origins of five consecutive tentacular lamellae, transverse section; Mallory's Triple stain (ML); C, Tentacles, distal free ends; Grenacher's Borax Carmine/Fast Green; D, Tentacles, fused as a lamella, cross-section (ML); E, Tentacle, free, showing connection of transverse intraepithelial loop with longitudinal tentacular blood vessel (arrow), trending toward adjacent pinnule, cross-section (ML); F, Dorsal vessel in posterior vestimentum, immature specimen, transverse section; Paraldehyde Fuchsin; G, Tentacles, fused as a lamella, longitudinal section (ML); H, Obturacular vessel in obturacular matrix, transverse section (ML). AE: anterior extension of trunk coelom; CG: coagulated coelomic fluid, CL: cilia; CO: coelom; CT: compartmented tissue; CU: cuticle; DB: anterior branch of dorsal vessel; DV: dorsal vessel; FM: "feather" longitudinal muscle; LT: large tentacle; MO: muscle strands of obturacular matrix; NT: neurular tube; OV: obturacular vessel; PM: parasagittal muscle; PN: pinnule; PV: perivascular cavity; RM: ring muscle; TC: tentacular coelom; TE: tentacular epithelium; TL: vessel from tentacular lamella "2"; TP: trophosome; TS: testes; TV: tentacular vessel; VB: anterior branch of ventral vessel; VL: intraepidermal transverse vascular loop; VM: ventral mesentery; VN: ventral nerve; VV: ventral vessel; X: site of formation of newest "compartment"; 1–5: serially more proximal tentacular lamellae. Scale bars (lower right)—A, B, F: 0.5 mm; C: 250  $\mu$ m; D, H: 100  $\mu$ m; E: 25  $\mu$ m; G: 50  $\mu$ m.







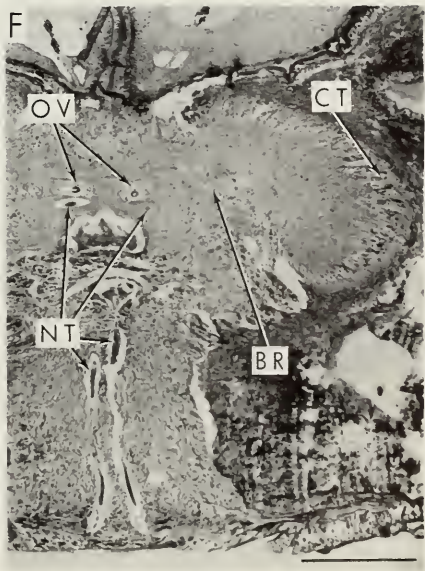
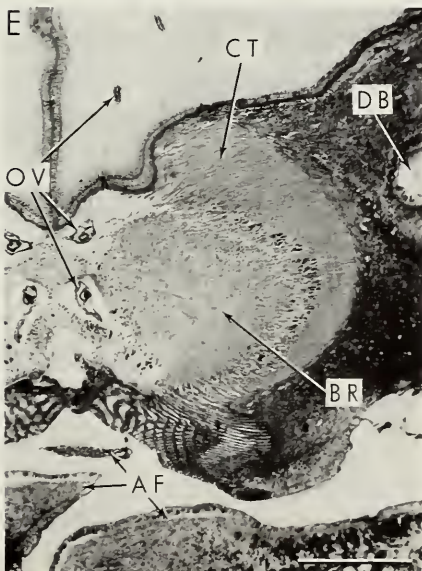
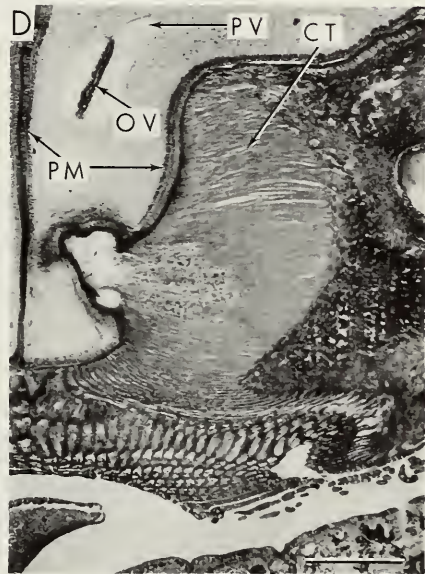
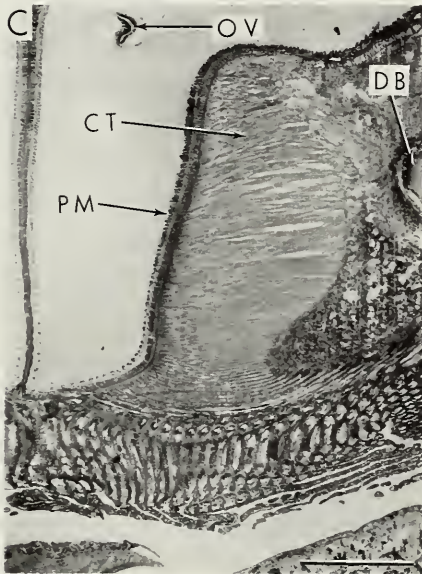
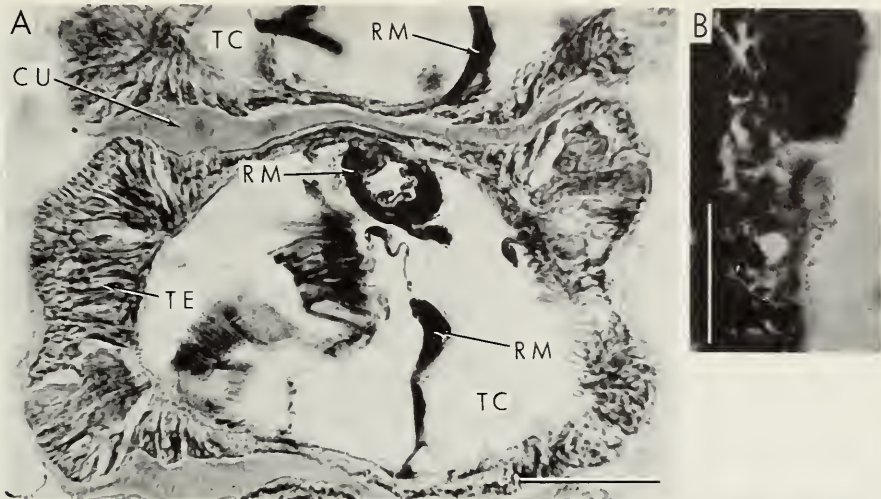
flanges; tube secretion adhering to solid materials (rocks, limpet shells) and to other tubes (Fig. 1A); in longer tubes, basal partitions separating worm's living space from unoccupied, basal, older portions (tube, presumed that of holotype, 2,654 mm long with basal end ragged, as if torn; at 1,245 mm from apical end of tube, secreted partition restricting occupant to distal portion of tube; between this partition and basal end, 11 partitions previously secreted).

Internally, obturaculum with gelatin-like, semi-solid matrix invested with thick cuticle (Fig. 2B, C); sagittal fusion of obturacular halves with double layer of cuticle; internal from cuticle as many as 500 bundles of muscles, appearing to be longitudinal, actually as many as 250 muscle rings, in parasagittal planes (Figs. 2C, 3B, 4C, D:PM); matrix penetrated by paired obturacular blood vessels, blind-ending near split anterior region of obturaculum, originating from two anterior branches of dorsal vessel in vestimental region (Figs. 2B, C, 3H, 4C-F); obturacular vessels with thin inner lining of muscle cells, then thick layer of connective tissue, surrounded externally by closely applied ring muscles (Fig. 3H); vessels supported by two mesenteric-like structures in perivascular cavity, lacking connection to any other body cavity. Vestimental region quite solid with mass of muscle strands and connective tissue elements intermixed (Fig. 3F); with close-packed pyriform glands in discrete layer, opening to external surface of overlapped flaps (dorsolateral) and vestimentum, proper (lateral and ventral) (Fig. 2A); brain anteroventral, internal to ventral overlapping of flaps; ventral extension of brain tissue extending to cuticular covering of body, containing paired neurular tubes arising *de novo* in brain tissue (Fig. 4F); ventral ciliated field formed of transversely fused cilia, emerging from epithelial cells not continuously in contiguous contact, forming considerable lacunae or sinuses; dorsal surface of posterior  $\frac{1}{4}$  of vestimentum with anterior extension of trunk and its coelomic cavities overlapping, with genital ducts moving for-

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Fig. 4. *Riftia pachyptila* (A-F: USNM 59953). A, Tentacles, fused as a lamella, showing contracted ring muscle (center) and two relaxed ring muscles (above and below), cross-section; Mallory's Triple stain (ML); B, Seta in body wall of opisthosome, frontal section; Mayer's Hematoxylin-Eosin; C, Compartmented tissue near base of obturaculum, transverse section (ML); D, Same, more posterior, showing beginning of transformation of compartmented tissue; bulge to left is initiation of connection of tissue to other side; transverse section (ML); E, Same, yet more posterior, with more extensive transformation of compartmented tissue to brain tissue; connection of both halves complete; transverse section (ML); F, Brain at level of descent of nerve tissue to form ventral nerve, transverse section (ML). AF: anterior "flap" of vestimental wing; BR: brain; CT: compartmented tissue; CU: cuticle; DB: anterior branch of dorsal vessel; NT: neurular tube; OV: obturacular vessel; PM: parasagittal muscle; PV: perivascular cavity; RM: ring muscle; TC: tentacular coelom; TE: tentacular epithelium. Scale bars (lower right)—A, B: 25  $\mu$ m; C-F: 0.5 mm.





ward then dorsally to open through genital apertures; excretory organ (possibly paired) posterior and ventral to brain. Trunk with internal surface of body wall with longitudinal "feather" muscles (van der Land and Nørrevang, 1975, 1977) internal to thin layer of more conventional longitudinal muscles, in turn internal to thin layer of mixed circular muscle and connective tissue, separated by basement membrane from layer of epithelial cells covered by external cuticular layer (Figs. 2F, G, 3A); paired coelomic cavities extending throughout entire length of trunk, separated by medial dorsoventral mesenteries investing dorsal and ventral blood vessels, attached to but not investing centrally located gonad and "trophosome" (van der Land and Nørrevang, 1975, 1977) (Figs. 2G, 3A); internal broad bases of pyriform glands project centripetally between rows of feather muscles (Fig. 2G:PG). Opisthosomal segments separated internally by two-layered septa; with only "normal" longitudinal muscles, "feather" longitudinal muscles lacking; segmental cavities separated medially by dorsoventral mesentery; anterior faces of septa with two kinds of glands, short broad and long slender, histologically different from pyriform glands of vestimentum and trunk; long slender glands invested by blood vessels which interconnect with other similar vessels and move centripetally to center of septum; segments also with low, thin, multilayered circular bands of muscles forming "partial septa" (Fig. 2E); ventral nerve here, well-formed, rounded, lacking neurular tube.

Tentacles covered with cuticle of varying thickness throughout length; fused basally for from 50 to 75% of their length to form tentacular lamellae, with tips of tentacles free (Fig. 2B); with two rows of multiciliated epithelial cells, one on posteroventral face, other on anterodorsal face, extending about 90% of basal length of each tentacle (Fig. 3D); with two rows of multicellular pinnules on posterior surface of each tentacle, along distal 45% of length, not extending to tips (Fig. 3C); central tentacular coelomic (?) cavity with two blood vessels, enclosed by basement membrane of single layer of epithelial cells (Fig. 3D, G); blood vessels connected along tentacular length by transverse intraepithelial vascular loops communicating with central cavities of pinnules (Fig. 3E); no nervous tissue seen; as many as 340 tentacles per lamella and 335 lamellae on each side of obturaculum (in holotype), about  $2.28 \times 10^5$  tentacles in plume; along length of each tentacular blood vessel "O"- or "U"-shaped ring muscles appear to act as series of sphincters (Figs. 3G, 4A); in basal region of lamellae, cuticle of fused tentacular bases thickened, successive lamellae fused to one another for short distance, serially (Fig. 3B:1-5); internally, cuticular matrix disappears and blood vessels of all tentacles of a given lamella join single transverse blood vessels which join anterior axial extensions of dorsal and ventral vessels of main body (Fig. 3B: DB, VB); immediate fate of coelomic tentacular space and of presumed tentacular nerves obscured and unknown; basal contents of all tentacles of given lamella unite, and their residuum



moving centrally, forming thin layer directed posteriorly toward base of obturaculum, in company with residua of more apical tentacular lamellae (Fig. 3B: X, CT); up to three tentacles of some lamellae lacking both rows of cilia and rows of pinnules, with 50% larger diameter and up to twice length of "normal" tentacles (Figs. 1C, 2B, 3C, D).

Dorsal vessel in trunk thin-walled with thin connective tissue layer covered with thin layer of circular (?) muscles (Fig. 2G); connecting branches to trophosome, mesenterial and other vessels traversing medial mesentery; heart body (*corpus cardiacum*) in dorsal vessel in midtrunk region; anteriorly, at level of anterior extension of trunk into vestimental region, dorsal vessel with thin muscle lining, with succeeding thick layer of connective tissue, surrounded by layer of striated, circular, ring muscles, supported in perivascular cavity by thickened dorsal and ventral mesentery-like structures, whole complex supported by second dorsoventral mesentery in anterior extension of trunk coelom (Fig. 3F); more anteriorly, in vestimental region, connective tissue layer of dorsal vessel lost, wall of apparently un-oriented muscle fibers, free in perivascular cavity (mesenteries lost), trunk coelom not present; perivascular cavity surrounding dorsal vessel not connected to trunk coelom or any other coelomic cavity; just posterior to level of brain, dorsal vessel branching, each branch moving anteriorly to run length of obturaculum, ventromedially, receiving single vessels from transverse tentacular lamellar vessels (Figs. 3B, 4C, E: DB); at level of branching, dorsal vessel giving rise to paired obturacular vessels, ending blindly near anterior margin of splayed obturaculum, undergoing up to 25 dorsoventral loops through obturacular matrix (Figs. 2B, C, 3H, 4C-F). Anterior branches of ventral vessel run length of obturaculum, ventrolaterally, in company with branches of dorsal vessel, receiving branches from each transverse tentacular lamellar vessel (Fig. 3B); at base of obturaculum, posterior to level of brain, branches unite, possibly forming valve of some kind, proceeding posteriorly as single vessel embedded in loose connective tissue, with no muscular layer. Fate of anterior branches of dorsal and ventral vessels unknown—perhaps blind-ending or connecting near anterior margin of obturaculum.

Blood directly from dorsal vessel of living animals, two hours after collection, in laboratory of surface ship, of dark red color and viscosity of port wine; coelomic fluid from trunk and opisthosome of similar color and viscosity.<sup>2</sup>

Residua of tentacular lamellae moving to bases of obturacula, augmented

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<sup>2</sup> The following papers concerned with the blood of *Riftia pachyptila* have been submitted to Science, as of this writing: A. Arp and J. Childress, observations on the functional aspects of oxygenation characteristics of extracellular hemoglobin; and J. Wittenberg, R. Morris, Q. Gibson, and M. Jones, data on the kinetic constants for combination and dissociation rates of the hemoglobin.

by residua of successively more basal tentacular lamellae, forming paired ventromedial masses of narrow compartments (Figs. 3B, 4C: CT); in anterior part of vestimentum, rigid linearity of compartments breaking down and lamellar residua becoming "transformed" into brain tissue (Fig. 4D, E); just anterior to branching of dorsal and ventral vessels, "pillar" of nervous tissue with paired neurular tubes, each in own cavity, moving ventrally to just internal to cuticle, becoming flattened to form band of nervous tissue with separated neurular tubes (Fig. 4F); posteriorly, band of nervous tissue branching laterally at about 10% length of vestimentum, and area between branches of ventral nerve, ventral ciliated field (Fig. 1D, E); at about 60–70% of length of vestimentum, divergence of nerve bands (and width of ventral ciliated field) at maximum, followed by rapid convergence of nerve tissue and neurular tubes, meeting at about 85% vestimental length, at posterior margin of ventral ciliated field; ventral nerve band continuing as such, with single neurular tube, to the posterior end of trunk (Fig. 3A); in opisthosome ventral nerve changing from band-like to compact, rounded cord, lacking neurular tube, proceeding to basal end of opisthosome (Fig. 2D).

Presumed excretory organ just posterior to brain at level of branching of dorsal and ventral vessels; main mass of ciliated tubules with no obvious separation into halves at mid-line; tubules with no apparent orientation, no apparent internal openings, uniting with other tubules and opening into non-ciliated cavities joining with others forming paired, non-ciliated canals, moving anterolaterally, then dorsally, at level of anterior margin of vestimentum, then opening into basal area of dorsal groove of obturaculum by paired excretory pores.

Sexes separate; single external morphological difference—ciliated grooves anterior from paired male genital apertures, lacking in females; paired genital apertures of both sexes on dorsal surface at approximately same location, about 70% vestimental length; eggs just inside female aperture at germinal vesicle stage, about 78  $\mu\text{m}$  diameter, spherical except for slight distortion due to packing; sperm just inside genital aperture with elongate bodies, corkscrew-shaped, about 9  $\mu\text{m}$  long, 0.6  $\mu\text{m}$  diameter, tails about 9  $\mu\text{m}$  long; no spermatophores seen; sperm ducts with ridge of epithelium along length; no eggs or developing embryos or larvae found in tubes of either females or males; none found in dorsal cavity formed by overlapping vestimental wings.

Trophosome of many lobules with central lumina, well-vascularized, with vascular plexi and lacunae over surfaces;<sup>3</sup> blood vessels forming lumina

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<sup>3</sup> The following papers concerned with the trophosome of *Riftia pachyptila* have been submitted to Science, as of this writing: H. Fehlbeck, an account of enzymes possibly attributable to the trophosomal bacteria; G. Rau, data on <sup>13</sup>C to <sup>12</sup>C ratios pertaining to these bacteria; and C. Cavanaugh, S. Gardiner, M. Jones, H. Jannasch, and J. Waterbury, a description of and observations on these organisms.



from which capillaries ramify throughout lobular mass; "tissue" of trophosome actually close-packed bacteria; surface of trophosomal lobules with numerous fine pigment granules/spots; trophosome in intimate association with gonads and gonoducts (Fig. 2G); trophosome of most specimens with crystals of free elemental sulfur in "tissue"; trophosome present in juvenile as small as 1.44 mm total length (USNM 59961).

In smallest juvenile (USNM 59963), total length 0.75 mm, no mouth, no gut, no anus; setae in two rows on opisthosome identical to setae of adults but of smaller size.

*Color in life.*—Obturacular region: tentacles, red; obturaculum, whitish, occasionally with greenish tinge; dorsal groove with white margins, interior, pink; ventral ridge, white; splayed apical surfaces pink with dark red obturacular vessels near surface. Vestimental region: anterior dorsal margin with green suffusion; inner and outer surfaces of overlapped flaps, red; ciliated tracts of male, brown/green; ventrally united anterior nerve, green; separated nerves at level of ciliated field, white with lateral red lines; united posterior nerve, green; ventral ciliated field, dark red; papillae, beige against pinkish beige background. Trunk: beige to pink beige, with green line on anterior dorsal surface at junction with vestimentum. Opisthosome: pink/dark red.<sup>4</sup>

*Faunal associates.*—Other animals present with *Riftia* in the immediate vicinity of the geothermal vents include *Calyptogena magnifica* Boss and Turner (vesicomid clam), *Bythograea thermydron* Williams (crab), a mytilid mussel, several shrimp, several limpet-like gastropods, a number of calanoid, cyclopoid, and harpacticoid copepods, at least six families of polychaetes, and a brotulid fish. Of these, the crab and the several shrimp appear to be predators on *Riftia*, based on direct observations (*vide* J. Childress).

*Feeding.*—The obturacular plume of *Riftia*, with its elaborate vascularization, would seem to be the most likely site for the uptake of at least small organic molecules. The extreme number of tentacles, each with up to 100 pairs of transverse intraepidermal vascular loops and the large cumulative surface of the vascularized pinnules (up to 100 pairs on each tentacle), comprise an admirable organ for molecular uptake. There is a possibility that similar uptake takes place across the body wall of the trunk, but nutrients would have to be carried in the water in the tube; due to the thickness of the tube wall, ruling out a diffusion across this wall, and the fact that such water could be renewed only during the occasional withdrawal of *Riftia* into its tube, this alternative seems much less likely. The trophosomal bacteria may also play a role in the nutrition of *Riftia*. The similarity of ratios of <sup>13</sup>C to <sup>12</sup>C in the trophosome (bacteria) and in the vestimental musculature

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<sup>4</sup> Color observations were made on specimens returned to the surface vessel laboratory, about two hours after collection; the worms probably were moribund at the time.

found by Rau (personal communication) suggests that *Riftia* may utilize the bacteria and/or their metabolites as a source of organic carbon.

*Comparisons.*—*Riftia pachyptila* is closely related to the recognized vestimentiferan species *Lamellibrachia barhami* Webb (1969a) and *L. luymesii* van der Land and Nørrevang (1975). The presence of an obturaculum with its associated tentacles basally fused to form tentacular lamellae (Figs. 1B, 2B), with the presumed excretory ducts on the anterodorsal margin of the vestimentum near the base of the obturaculum, the presence of the vestimentum with its dorsolateral flaps (Fig. 1B), with a ventral ciliated field set off by a bifurcation of the ventral nerve (Fig. 1E), with both female and male genital apertures opening on the posterodorsal surface of the vestimentum from an anterior extension of the trunk, with a trunk containing an extensive trophosome and primary longitudinal muscle of the "feather" type (Fig. 2F, G), and with neurular tubes in association with the ventral nerve (Figs. 3A, 4F), all leave no doubt as to this relationship. Unfortunately, there was no opportunity to compare the opisthosome of *Riftia* with those of either species of *Lamellibrachia*, for in the one case (van der Land and Nørrevang, 1975) the opisthosome was lost at the time of collection; in the other case (Webb, 1969a) a detailed description has yet to be recorded and this account leaves me with some doubt as to whether the opisthosome has actually been observed. I have had the opportunity to examine specimens of *L. barhami* deposited here by E. Barham (USNM 55162), comprising part of his original collection. In all specimens examined, the posterior ends, usually 1 mm or less in diameter, were either poorly preserved or had dried and were flattened against the inner surface of the tube; I was, thus, unable to identify an opisthosome in these specimens. I have also examined specimens of *L. barhami* collected by trawl by A. Carey, Oregon State University, 30 Oct 1967, at 1,400–1,600 m depth, at about 44°35.7'N, 125°11.0'W (in part, USNM 61103). The posterior ends of these specimens, also, appear to have been poorly preserved or to have dried so that confirmation of an opisthosome was not possible.

Of the differences so far observed in comparing *R. pachyptila* with the descriptions of both species of *Lamellibrachia* and with specimens of *L. barhami*, the following characters of *Riftia* are deemed to be of most importance. Obturacular region: Tentacular lamellae are free from one another for most of their length (Fig. 1D); tentacular lamellae arise perpendicularly from the obturaculum (Fig. 1D); there are no "tentacular sheaths" (Webb, 1969a; van der Land and Nørrevang, 1975, 1977); obturaculum comprises no less than 11% of the total length (Table 1). Vestimental region: Bears two separate and distinct external openings of the ducts from the presumed excretory organ(s); vestimentum may comprise from 7 to 22% of the total length of young or older adults (of greater than 50 mm total length) (Table 1). Tube: With one opening, nearly cylindrical, with very little tapering



Table 2.—Comparison of diagnostic characters of Lamellibrachiidae Webb and Riftiidae new family.

	Lamellibrachiidae	Riftiidae
Orientation of tentacular lamellae	Axial, parallel to obturaculum	At right angles to obturaculum
Tentacular sheaths	Present	Absent
Relative length of obturacular region	4% total length	10% total length
External opening(s) of excretory ducts	One	Two
Shape of tube	Tapered	Essentially cylindrical

toward the closed basal end (Fig. 1A). Taken as a whole these differences suggest that *Riftia* should be separated from *Lamellibrachia* at the familial level (Table 2).

Although the arguments of van der Land and Nørrevang (1975, 1977) are persuasive and their points are well-taken, at the present time, I must consider the basic regionation of *Lamellibrachia* and *Riftia* as indicating a close relationship with the frenulate Pogonophora. The presence of demonstrable coelomic cavities in the first and second regions of the latter and the absence of such in *Lamellibrachia* and *Riftia* might well be a consequence of the development of the solid obturaculum and the heavy muscularization of the vestimentum. Other differences, e.g., the vestimental wings, the presence of the trophosome, neurular tubes, and multicellular pinnules, the absence of spermatophores, the medial dorsoventral mesentery of the opisthosome, the tube morphology, in my present view, might be accommodated by considering them to discriminate between subphyla. While this decision might appear to be somewhat frivolous or gratuitous, I feel that it best summarizes my view of the relationship of *Riftia* and *Lamellibrachia*, with respect to the other pogonophorans, i.e., it admits the unifying character of the basic body plan of four regions, but emphasizes the exceptional and unique differentiating characters listed above. Further studies of *Riftia* and *Lamellibrachia* may temper my judgement in this respect, but for now, I here propose two subphyla for the phylum Pogonophora: **Obturata** new subphylum (from Latin, *obturo* (close up, stop up), in reference to the operculum-like function of the obturaculum of *Lamellibrachia* and *Riftia*); and **Perviata** new subphylum (from Latin, *pervius* (affording a passage, open, penetrable), in reference to the lack of an operculum-like structure in the remaining pogonophorans).

Concerning the relationships of the Pogonophora I concur with van der Land and Nørrevang (1975, 1977), Southward (1975a, b), and George (1973)

in considering the phylum to be most closely related to the phylum Annelida. The opisthosome, with its repeated similar segments provided with chitinous setae, as well as the morphology of the latter, is the single most compelling feature contributing to my conclusion.

There is no question that all vestimentiferan specimens from the various geothermal vents of the Galápagos Rift are *Riftia pachyptila*. I am less certain of the identity of the single specimen available from the East Pacific Rise; superficially there is little difference between this specimen and those from the Galápagos Rift, some 3,400 km distant. So far I have not chosen to dissect this single specimen; more material should be available from the Rise area in the coming year, when a detailed examination should shed light on the taxonomic status of the northern specimens. The relatively large obturacular region (Table 1, USNM 59964) suggests that a different species may be present there, but for now, I must conclude that *Riftia* is a monospecific genus.

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Division of Worms, Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.